Tree Physiology 28, 1407–1419

Within-canopy sampling of global irradiance to describe downwelling light distribution and infer canopy stratification in a broadleaf forest

RITA GIULIANI[1–3] and KIM J. BROWN[1]

[1] *Department of Environmental and Plant Biology, Ohio University, Athens, OH 45701, USA*

[2] *Present address: CNRS-CEFE, 1919 Route de Mende, 34293 Montpellier Cedex 5, France*

[3] *Corresponding author (rita.giuliani@cefe.cnrs.fr)*

Received October 5, 2007; accepted February 20, 2008; published online July 1, 2008

Summary A broadleaf mixed forest diversified through partial tree thinning was studied to identify expedient sampling and data analysis procedures to capture the heterogeneous within-canopy downward distribution of instantaneous global photosynthetic photon flux (PPF); to extract foliage structural properties from the acquired light values; and to compute statistics descriptive of the within-canopy light and leaf layer distributions. We sampled PPF at 1-m intervals along vertical gradients using a helium-filled balloon as a platform for a light sensor. A random method was used to identify the forest floor locations for the within-canopy balloon ascents. About 400 PPF measurements were recorded per vertical transect. For each PPF value, we computed, by inversion of the Monsi-Saeki model, the number of leaf strata cumulated along the sunbeam direction from the position where the light was measured. Variability in PPF and leaf layer at different vegetation scales was computed by non-parametric statistics. The methods were evaluated as appropriate for intra-canopy PPF sampling, particularly in an undisturbed canopy. The minimum number of vertical PPF profiles required to capture the within-canopy PPF variability was 9–10 (equivalent to about 4000 measurements). The reliability and sensitivity of the inversion of the Monsi-Saeki method were sufficient to capture the canopy structural differences between undisturbed and partially thinned forests. The proposed PPF canopy sampling and data analysis procedures provide a fast, reliable and inexpensive way to characterize tree crown structure, and to predict plant growth and forest dynamics and could be applied whenever vegetation absorbed radiation is a main driving force for forest canopy processes. The experimental light attenuation data and the extracted canopy leaf layer numbers could serve to corroborate canopy mechanistic models of radiative transfer and net primary production.

Keywords: Beer-Lambert equation, canopy geometry, canopy light interception, Carya, cluster analysis, helium-filled balloon, leaf strata, oak–hickory forest, Quercus.

Introduction

Solar radiation within the 400–700 nm waveband (photosynthetic photon flux, PPF) drives the photosynthetic process, and global radiation (300–2500 nm waveband) provides the energy for transpiration activity (Nobel 1991). Plant canopy geometry determines the spatial and temporal interaction between incoming radiation flux and foliage, and therefore plays a central role in quantifying the driving force for leaf physiological processes (Monteith and Unsworth 1990, Jones 1992, Jurik and Kliebenstein 2000, Parker et al. 2002).

No fast and convenient direct method with a high spatial resolution has yet been developed to characterize the complex canopy geometry of a forest stand. However, new laser-based technologies (Lefsky et al. 2002, Parker et al. 2004*a*, 2004*b*, Houldcroft et al. 2005) are being developed to provide detailed descriptions of canopy architecture at the forest scale (Wulder and Franklin 2003), whereas imagery remote sensing has been applied more at the single-tree level (Shlyakhter et al. 2001, Phattaralerphong and Sinoquet 2005) than at the stand level (Couteron et al. 2005).

Leaf area index (LAI) is often used to represent canopy structure and to model within-canopy radiative transfer and foliage functions. Several direct and indirect methods are available to estimate LAI (Pierce and Running 1988, Norman and Campbell 1989, Hanan et al. 2002, Bréda 2003, Jonckheere et al. 2004, Weiss et al. 2004, Ericksson et al. 2005). For example, LAI can be retrieved from estimates of gap fraction (Rich 1990, Martens et al. 1993, Chen 1996) or sunfleck size distribution (Miller and Norman 1971, Chen and Cihlar 1995, Chen 1996), and remotely sensed from the ground by optical methodologies.

The mathematical modeling of within-canopy radiation transfer is commonly based on the seminal equation proposed by Monsi and Saeki (1953), which makes it possible to simulate the downwelling radiation extinction based on the Beer-Lambert exponential law. Contradicting general empirical knowledge, the Monsi-Saeki equation relies on the simplified geometrical assumption of a canopy composed of infinitesimally small horizontal leaves randomly distributed and oriented in the entire canopy space, and on the simplified optical assumption of the vegetation as a homogeneous turbid medium. Because, in reality, the spatial distribution of the canopy leaves violates the theory of the Monsi-Saeki function (Anderson 1966), this model is usually applied in a modified form to accommodate a preferential leaf inclination angle distribution and a leaf aggregation parameter (leaf clumping index, Ω), but still with considerable simplifications in the assumed structure of the vegetation.

Besides the inclusion of LAI as a canopy structural feature, a canopy light extinction coefficient (*K*) that depends on leaf inclination angle distribution (and that parameterizes the complex geometric interaction between canopy leaf blades and incident sunbeams) is implemented in the Monsi-Saeki equation (Ross 1981, Norman and Campbell 1989). Based on theory, $K = 1.0$ is associated with canopies composed of horizontal leaves, and $0.5 \le K \le 0.7$ may be a reasonable approximation for a wide range of broadleaf canopies (Norman and Campbell 1989). An ideal canopy with random leaf dispersion has $\Omega = 1.0$, and Ω decreases as leaf clumping increases and it is also affected by solar elevation angle (Chen 1996, Leblanc et al. 2002). Optical remote sensing methods are generally used to estimate *K* (Chen et al. 2005, Sinclair 2006) and Ω (Chen and Cihlar 1995, Kucharik et al. 1999, Mõttus 2004, Leblanc et al. 2005).

The accuracy of a modified Beer-Lambert law model (Jurik and Kliebenstein 2000, Parker et al. 2002, Wang 2003) is affected by the magnitude of the direct and diffuse radiation components (Vezina and Pech 1964, Miller and Norman 1971, Spitters et al. 1986, Jones 1992, Roderick et al. 2001), and depends on the representativeness of the implemented canopy structural traits (Whitehead et al. 1990, Brown and Parker 1994, Gastellu Etchegorry et al. 1996, Wu et al. 2000, Jacquemoud 2004, Teske and Thistle 2004, Smolander and Stenberg 2005, Kitajima et al. 2005, Disney et al. 2006).

Direct instantaneous measurements of forest within-canopy radiation fluxes may be made by sensors mounted atop telescopic poles, helium-inflated balloons or a platform suspended from the gondola of a tower crane (Parker et al. 2002). A crucial point when performing within-canopy direct radiation flux sampling is to identify a suitable measurement plan to capture the spatial variability with sufficient resolution and in the shortest time. Besides the several systematic sampling schemes that have been used in various forest research contexts (Ghosh and Innes 1996, Shiver and Borders 1996), a simple random (Thomas and Winner 2000), stratified random (Dessard and Bar Hen 2005), or semi-random sampling technique (Sakai and Akiyama 2005) may be applied. In addition, non-parametric statistical techniques such as cluster analysis (Kaufman and Rousseeuw 1990) and bootstrap (Efron and Tibshirani 1993) may be appropriate to describe and scale up experimental information obtained from local data samples.

The availability of intra-canopy radiation measurements of *K* and Ω parameters makes it possible to invert the Monsi-Saeki light attenuation model to infer canopy leaf strata (Pierce and Running 1988). Application of the Monsi-Saeki function to extract information on leaf layers may be considered convenient for its simplicity, although the same canopy structural complexity responsible for the bias in the within-foliage light attenuation by the Beer-Lambert law contributes to the imprecision of the computed canopy leaf strata. In particular, the light extinction exerted by woody material (stems and branches) should be quantified to avoid overestimation of the number of leaf strata by the Monsi-Saeki function. Given the woody area index (WAI) as half total wood surface area projected per unit ground area, and the plant area index (PAI) as leaf plus wood area indexes, a WAI:PAI correction value could be applied, assuming a wood distribution similar to that of foliage (Kucharik et al. 1998, Law et al. 2001). The Monsi-Saeki model inversion precludes any possibility to compute horizontal and vertical leaf area density profiles (Parker and Brown 2000). However, Parker et al. (2002) showed that, in a Douglas-fir forest, the output of the inversion of the Beer-Lambert model provided a canopy LAI close to the LAI estimate obtained by a leaf intercepting method along a randomly chosen vertical line through the canopy (Thomas and Winner 2000).

Our study had three objectives. (1) To define an expedient sampling procedure to capture the canopy downwelling distribution of instantaneous global PPF through a broadleaf mixed forest. (2) To extract canopy leaf strata cumulated along the sunbeam path (*L*) from the PPF dataset: specifically, each PPF value was inverted by a modified version of the Monsi-Saeki model to extract the number of leaf strata that attenuate direct radiation and are responsible for that measured PPF value. (3) To describe the within-canopy variability in PPF and *L* at different vegetation scales by non-parametric statistical techniques.

Materials and methods

Study site

The trial was conducted in the Zaleski State mixed deciduous forest located in south-eastern Ohio (39°3′ N, 82°6′ W) in a hilly area at 350 m minimum elevation and with a mean slope of 15.7°. The forest stand mainly comprises oak and hickory species (*Quercus* and *Carya* spp.), with uneven-aged trees having canopy heights from 21.0 to 33.0 m and a modal dominant height of 25.0 m.

A land surface of about 1.0 km^2, already serving a silvicultural network investigation (FFS Ohio Hills Study Site, http://www.fs.fed.us/ffs/docs/ohio/) was chosen for the within-canopy global PPF measurements. The selected area hosts an undisturbed forest section and a thinned (35% of the trees removed) forest section. The undisturbed forest section has about 350 trees ha^{-1} with a trunk basal area (TBA) of 28.0 m^2 ha^{-1}, and the thinned section has 230 trees ha^{-1} and a TBA of about 20.0 m^2 ha^{-1} (Iverson et al. 1997).

Within-canopy downwelling global PPF detection

Measuring apparatus A cosine-corrected LI-190SA quantum sensor (Li-Cor) measured downwelling instantaneous global PPF (μmol m^{-2} s^{-1}) in the forest canopy. This sensor measures hemispherical incoming radiation and has a detecting surface area of 45.0 mm^2; however, when used within the foliage it acts as a point detector. The sensor was placed on the horizontal top surface of a helium-inflated balloon (Figure 1A) that lifted the sensor through the canopy in 1-m increments. At each selected canopy height, measurements were recorded every second by a HOBO H8 miniature data logger (Onset Computer Corporation, Bourne, MA) attached under the balloon.

Based on the apparatus built by Parker et al. (1996), the helium-inflated balloon was shaped as a parallelepiped with a 0.90 × 0.90 m base and a 1.60 m height plus a base contiguous pyramid with 0.65 m height (Figure 1B). The balloon was tethered from the pyramid apex (Figure 1E), so that the top surface served as a platform for the radiation sensor (Figure 1A), and a spooler was used to roll up the tether (Figure 1F). The tether was 35.0 m long and was marked at 0.25-m intervals (from a starting value of 2.25 m corresponding to the height of the chamber) to identify the quantum sensor elevation while lifting the balloon through the canopy.

A custom-built device attached to the tether spooler was used to tag each recorded PPF measurement, making it possible to associate a canopy height to each PPF value. The height indicator system comprised a battery-driven linear potentiometer, a knob to select among 30 distinct voltage potentiometer outputs, a HOBO H8 data logger and an on/off switch (Figure 1G). At each balloon height stop, the corresponding knob position was selected and the switch was put in the off position, and its corresponding potentiometer voltage output recorded by the data logger. Conversely, while lifting the balloon, the switch was put in the on position: a short circuit occurred and a background signal (0.05 V) was stored. Before use, the data loggers recording the quantum flux data and storing the potentiometer voltage values were synchronized.

The balloon's top surface was kept horizontal by acting on the balloon's tether to maintain the tether parallel to a 3-m vertical reference pole inserted in the ground at a few meters from the forest floor location chosen for vertical light sampling. When the balloon was not in the correct posture, the corresponding recorded values were marked by choosing the on switch in the height indicator device, so that they could be recognized later and excluded from data processing. Under the reasonable assumption that a maximum inclination of ± 10° from the horizontal affected the top surface of the balloon, PPF variations associated with deviations from the ideal position were computed. A ± 12% maximum PPF divergence was calculated: this imprecision, given its random nature, its magnitude, and the context of our investigation, was considered negligible.

Radiation measurements Global PPF was measured in July and August 2003 under clear sky conditions, negligible wind conditions (a breeze of about 1.5 m s^{-1} was most times unavoidable) and within a 2-h period around solar noon, corre-

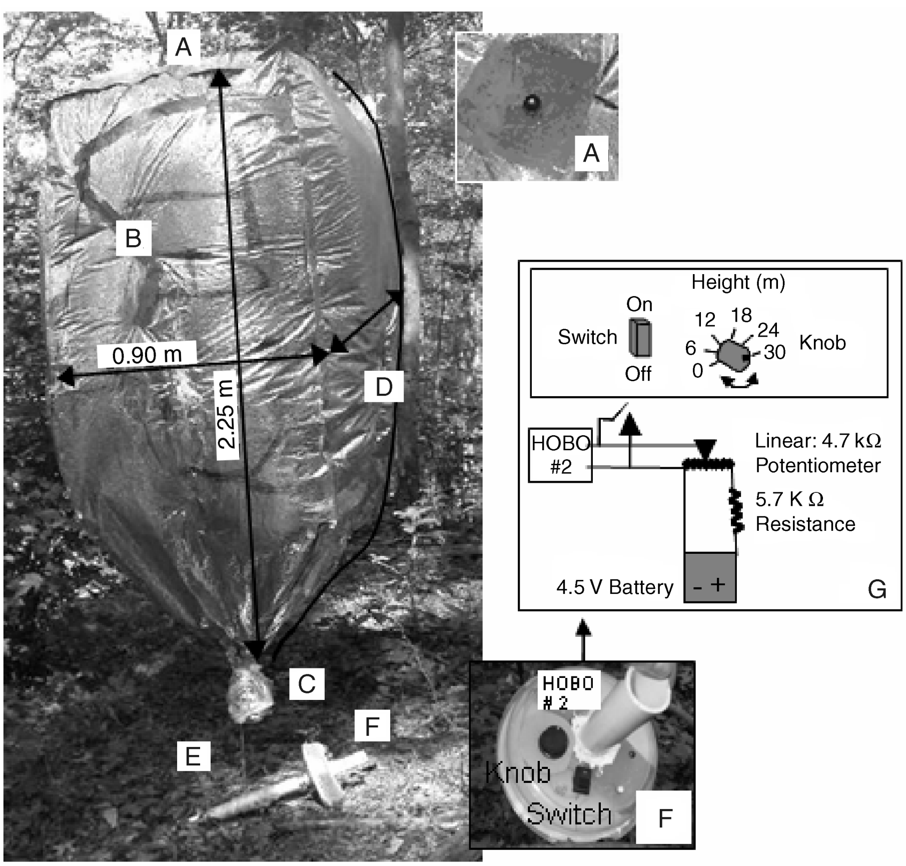

Figure 1. Components of the apparatus for measuring within-canopy photosynthetic photon flux: (A) LI-190SA quantum sensor; (B) helium-inflated balloon; (C) bag protecting the HOBO H8 data logger #1; (D) cable connecting the quantum sensor to the HOBO H8 data logger #1; (E) tether; (F) height indicator attached to a spooler with knob switch and HOBO H8 #2; and (G) electrical and front panel schemes of the height indicator.

sponding to a range of sun elevation angles from 58 to 72°.

In both undisturbed and thinned canopy sections, the balloon ascents were made from randomly selected forest floor positions. Specifically, a random seed instruction (rdn (x) in Mathcad 6.0, Mathsoft, Cambridge, MA) was adopted to generate two sequences of pseudo-random numbers in $0 < x < 1000$ and $0 < y < 1000$ intervals, where 1000 corresponded to the maximum length in meters on the two orthogonal East–West and North–South coordinates of the forest area map. The extracted couples of random numbers identified an X,Y uniformly distributed pseudo-random point series in each forest (Stoyan et al. 1995). The coordinates 0,0 were associated with the south-western corner of the forest area. The X,Y ground points were located by a global positioning system device. The tree cover dominating one identified ground position was too dense for the balloon to pass through, and the forest floor at another location precluded sampling from that point, so different forest floor stations for balloon raising were extracted in these cases.

A diagram of the intra-canopy vertical PPF sampling performed by raising the helium-filled balloon from the forest floor to above the tree cover is shown in Figure 2A. The balloon displayed some lateral movement during its ascent, exploring a circular area of 1.0 to 4.0 m^2 in relation to the canopy structure, mainly because the balloon sometimes had to be guided through gaps that were not on the desired vertical path.

Preliminary studies showed (1) the necessity of completing a balloon ascent within 15 min, and (2) that adequate vertical resolution was obtained from PPF measurements made at 1-m intervals provided the appropriate number of measurements were made. Therefore, the balloon was stopped at each meter height, from 3.0 m above ground, and between 15 and 40 PPF measurements were made at each height, enabling measurements of 2–3 vertical profiles in both undisturbed and thinned sections on each day.

In both forest sections, besides the vertical global PPF profiles, the balloon-mounted light-sensor measured a horizontal global PPF transect at about 3.0 m from the forest floor on a cloudless day in late July around solar noon by randomly walking the tethered balloon (Hughes 1996). A 20-min walk was taken at 0.5–0.6 m s^{-1} making it possible to record about 1200 PPF values while keeping the balloon in the appropriate posture. A simple random walk path was constructed according to the following rules: a starting point was randomly identified; a distance linear segment of 10.0 m was fixed; the trajectory of each segment was independently decided by random extraction of a turning angle (± 180°) to the previous trajectory, but excluding the directions driving the segment outside the explored forest section.

Statistical control of PPF sampling During measurements, the Kolmogorov-Smirnoff (K-S) test (Zar 1984) was executed to identify the minimum number of canopy vertical profiles necessary to capture the downward global PPF variability in the undisturbed and thinned forest sections. The cumulated relative frequencies of the PPF values collected at canopy heights of 3.0, 8.0, 13.0 and 18.0 m made it possible to assess, for each vegetation plane, if an additional data sample was adding a supplementary fraction of light variability. If the K-S test detected a significant statistical deviation ($\alpha = 0.05$) between the cumulated distributions of the radiation data captured at one canopy level before and after having implemented an additional data sample, a new vertical profile was monitored; conversely, if the number of captured data samples was considered sufficient the PPF data collection was stopped. We chose to employ a nonparametric technique to drive the within-foliage radiation sam-

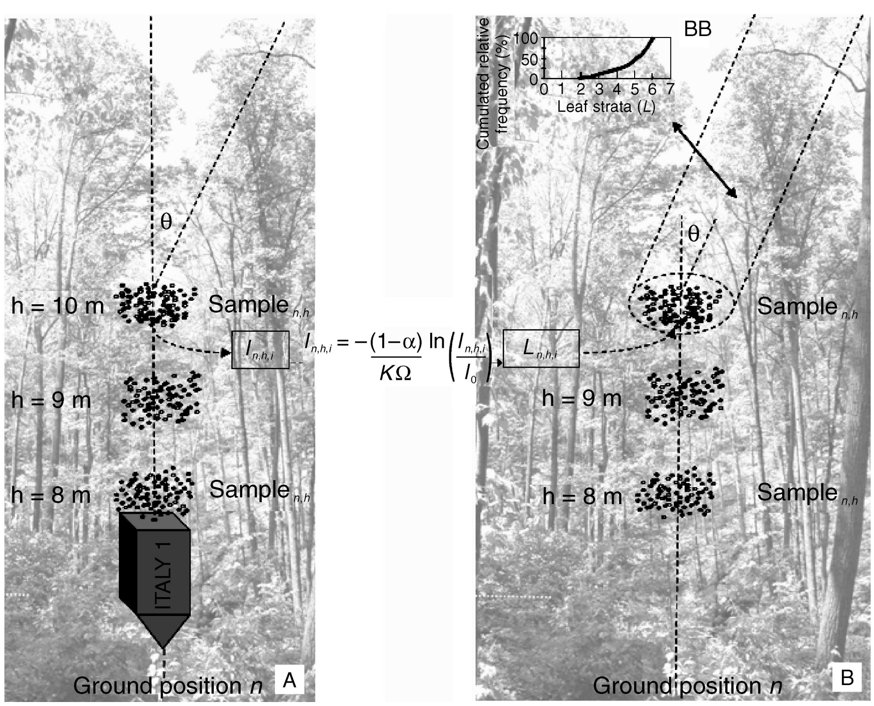

Figure 2. (A) Scheme of the within-canopy downwelling photosynthetic photon flux (PPF) sampling along the nth vertical transect. A quantum sensor was placed on the horizontal top surface of a helium-filled balloon that was lifted in 1-m steps until it was measuring above-canopy PPF. A sample of 15–40 PPF measurements (i) was acquired at each balloon height (h). (B) Each n,h,i PPF point measurement was used to compute, by inversion of the Monsi-Saeki model, the corresponding number of light attenuating leaf strata cumulated along the sunbeam direction from the n,h,i position toward the sun. (BB) At each canopy height in each vertical transect, the acquired PPF sample corresponded to a sample of leaf strata (L). The cumulated relative L distribution associated with h = 10 m in the vertical profile n is shown as an example.

pling procedure because of the generally observed skewed distribution of light data gathered at different canopy elevations (Baldocchi et al. 1985, Parker et al. 2002). Ten and nine vertical balloon transects were sufficient to describe the downwelling light attenuation in the undisturbed and thinned forest sections, respectively. Because a single vertical transect provided about 400 PPF measurements, about 4000 PPF values composed the dataset collected in each forest section.

In addition, a comparison of the cumulated relative frequencies of the PPF data recorded at 3.0 m height by vertical ascents and by random walking (assumed to capture all spatial light fluctuations) was performed by the K-S test ($\alpha = 0.05$). The two PPF distributions were similar in the undisturbed canopy ($P = 0.67$), whereas a significant difference was observed in the thinned canopy ($P = 0.038$). In the thinned forest section, the shaded and penumbral PPF frequencies cumulated at 3.0 m were underestimated by the balloon ascent technique compared with the horizontal random walk (Figure 3).

PPF data analysis

Because of the possible wide spatial heterogeneity in within-canopy instantaneous quantum flux (Baldocchi and Collineau 1994, Montgomery and Chazdon 2001), the PPF measurements made in the vertical and horizontal transects were considered independent. For each balloon ascent, the PPF samples were grouped in seven classes of 300 μmol m^{-2} s^{-1} amplitude: a contour plot was used to show the relative frequency of each PPF category in the vertical profile (e.g., see Figure 4).

The K-means non-hierarchic cluster analysis was applied to all available PPF samples (each composed of 15–40 values per vertical transect for each sampled canopy height) to group them in five clusters (see Figure 5). This statistical analysis required that the number of clusters be fixed a priori. The PPF cumulated relative frequency distributions associated with all acquired light samples were grouped based on statistical similarity. A representative PPF cumulative relative frequency distribution was identified for each cluster as the mean of all distributions included in that class. The 5, 25, 50, 75 and 95th percentiles representative of all PPF data collected at each canopy height in each undisturbed and thinned forest section were plotted (see Figure 6).

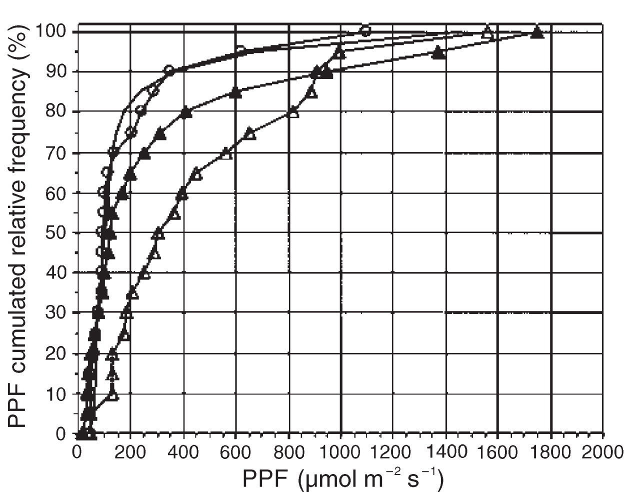

Figure 3. Cumulated relative frequency of photosynthetic photon flux (PPF) measured at 3.0 m in the undisturbed canopy by balloon ascent (continuous line) and by random walk (○), and in the thinned canopy by balloon ascent (△) and by random walk (▲).

Extraction of canopy directional leaf strata based on PPF inversion model

Monsi-Saeki model Within-canopy one-dimensional PPF attenuation can be modeled by a modified Monsi-Saeki exponential model:

$$I_{n,h,i} = I_0\, e^{\frac{-\Omega K L_{n,h,i}}{1-\alpha}} \qquad (1)$$

where $I_{n,h,i}$ is the ith PPF measurement in the vertical transect at ground position n at height h, I_0 is above-canopy PPF, $L_{n,h,i}$ is cumulated number of leaf strata responsible for the attenuated quantum flux in the n,h,i location, and α is the woody area to plant area index (WAI:PAI).

Estimates of Monsi-Saeki model parameters Leaf clumping index was estimated in a complementary trial (authors' unpublished data) carried out in both the undisturbed and thinned forest sections by ground-based upward optical remote detection. The radiation measurements necessary to perform gap fraction analysis leading to Ω computation (Chen and Cihlar 1995) were made with TRAC (3rd Wave Engineering, Ontario, Canada) equipment in July and August 2003 under clear sky conditions at solar elevation angles between 30 and 50°. For the 20 rectangular plots (50 × 20 m) sampled in both undisturbed and thinned vegetation sections, the TRAC device was carried by a person walking at a steady pace (about 0.3 m s^{-1}) along the 20 m side of each plot. The sensors were kept horizontal, and care was taken to avoid sensor shading with the body while walking. Because the plots differed in orientation, the measurement time in each of them was scheduled to allow the difference between the transect direction and the solar azimuth angle to be greater than 30° (Chen et al. 1997).

We adopted $K = 0.50$ on the assumption of a spherical canopy leaf angle distribution and consideration of the interval of solar elevation angles chosen for light measurements (Ross 1981, Macfarlane et al. 2007). The value $\alpha = 0.10$ was computed based on analysis of hemispherical photographs taken in the centers of the rectangular plots (authors' unpublished data).

Monsi-Saeki model inversion Given the availability of measured values of $I_{n,h,i}$ and I_0, Equation 1 was inverted to model $L_{n,h,i}$, which defines the number of light attenuating leaf strata cumulated along the sunbeam direction from each n,h,i measuring location toward the sun (Figure 2B):

$$L_{n,h,i} = -\frac{1-\alpha}{K\,\Omega} \ln\left(\frac{I_{n,h,i}}{I_0}\right) \qquad (2)$$

Values of $\Omega = 0.83$ for the undisturbed forest section and $\Omega = 0.80$ for the thinned vegetation section were adopted (authors' unpublished data), and values of $K = 0.50$ and $\alpha = 0.10$ were used for both forest sections.

For each measured canopy height in each vertical transect, the cumulated relative frequency distribution of L was descriptive of the geometrical interaction between the foliage included within the skewed cylinder directed toward the sun, based on the round surface inspected by the balloon sensor and the incoming PPF (Figure 2B).

Corroboration of extracted canopy directional leaf strata

The directional leaf strata estimated at 3.0 m height in both undisturbed and thinned forest sections were compared with the corresponding LAI values estimated by ground-based upward optical remote sensing and litter collection in a complementary study carried out in the Zaleski State Forest (authors' unpublished observations).

The LAI was inferred from LAI2000 (Li-Cor) measurements that were acquired in the centers of 10 plots (50 × 20 m) sampled in each undisturbed and thinned vegetation section. The LAI2000 measurements were taken under cloudy sky conditions keeping the device horizontal and about 2.0 m from the ground, with a 270° cap on its radiation sensor, and imposing a North view direction. The LAI computation for each explored location was performed with the LAI2000 software; with $\Omega = 0.80$ for the thinned and $\Omega = 0.83$ for the undisturbed forest sections, and $\alpha = 0.10$ for both forest sections.

Litter was collected with a trap placed in the center of each of the 10 plots then measured with the LAI2000 in both undisturbed and thinned forest sections, making it possible to estimate LAI directly.

Directional leaf strata data analysis

For each balloon ascent, L computed at each explored canopy elevation were grouped in seven classes of 1.0 amplitude, and a contour plot was used to show the relative frequency of each L category in the vertical profile (see Figure 7).

The K-means non hierarchic cluster analysis was applied to all available L samples, each comprising 15–40 values computed in each vertical transect for each canopy height, to group them in five clusters (see Figure 8). This required that the number of clusters be fixed a priori. The L cumulated relative frequency distributions associated with the computed L samples were grouped based on their statistical similarity. A representative L cumulative relative frequency distribution was identified for each cluster as the mean of all distributions included in that class. The 5, 25, 50, 75 and 95th percentiles representative of all L values inverted from the PPF data at each canopy height in the undisturbed and thinned forest section are shown (see Figure 9).

Results

PPF data

The relative frequencies of PPF classes for four balloon ascents, chosen as examples, are shown in Figure 4. Figure 4A shows a strong attenuation of PPF by the upper canopy so that most of the PPF data through the vertical profile were included in the category from 0 to 300 μmol m^2 s^{-1}. By contrast, Figures 4B–D show large PPF fluctuations throughout the canopy.

The results of the K-means cluster analysis applied to all within-canopy PPF measurements collected in both forest sections are shown in Figure 5. The undisturbed canopy mostly exhibited PPF classes from 0 to 300 and from 200 to 1000 μmol m^2 s^{-1}, whereas the thinned canopy showed a wider range of PPF values that included the classes from 200 to 700, from 700 to 1500, and from 1500 to 1750 μmol m^2 s^{-1}.

The 5, 25, 50, 75 and 95th percentiles representative of PPF values associated with the different canopy heights were plotted for both the undisturbed (Figure 6A) and thinned (Figure 6B) forest sections. In the undisturbed forest, median PPFs fluctuated from about 1800 to 700 μmol photons m^2 s^{-1} in the top canopy fraction down to 28.0 m height, whereas the 5–95th PPF percentile ranges showed a maximum of 1700 μmol m^2 s^{-1} (Figure 6A). Below a canopy height of 28.0 m, a sharp decrease in median PPF occurred followed by median fluctuations and a minimum value of 100 μmol m^2 s^{-1} was calculated at 14.0 m height. The canopy zone between 28.0 and 14.0 m height was characterized by wide variability in PPF and a maximum 5–95th PPF percentile range of about 1700 μmol

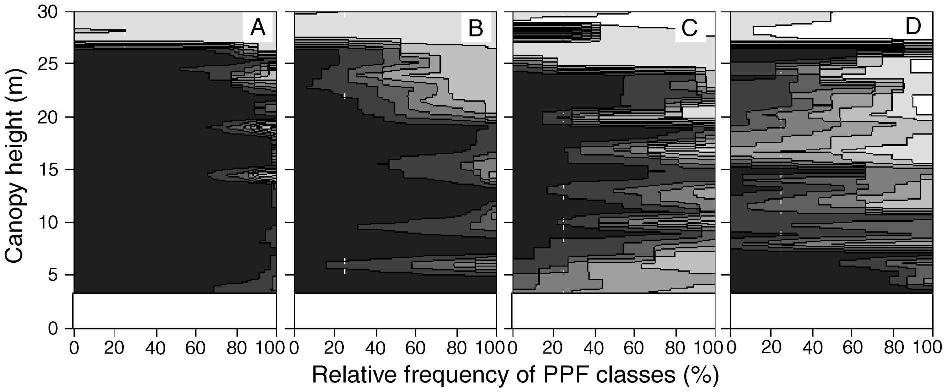

Figure 4. Example of contour plots showing the relative frequency of photosynthetic photon flux (PPF) classes for a canopy vertical light transect in an (A, B) undisturbed forest section and a (C, D) thinned forest section. Measurements of PPF started at 3.0 m above the forest floor. The gray scale corresponds, from black to light gray, to seven increasing PPF classes with amplitude of 300 μmol m^2 s^{-1} each. Values between canopy height increments are interpolates.

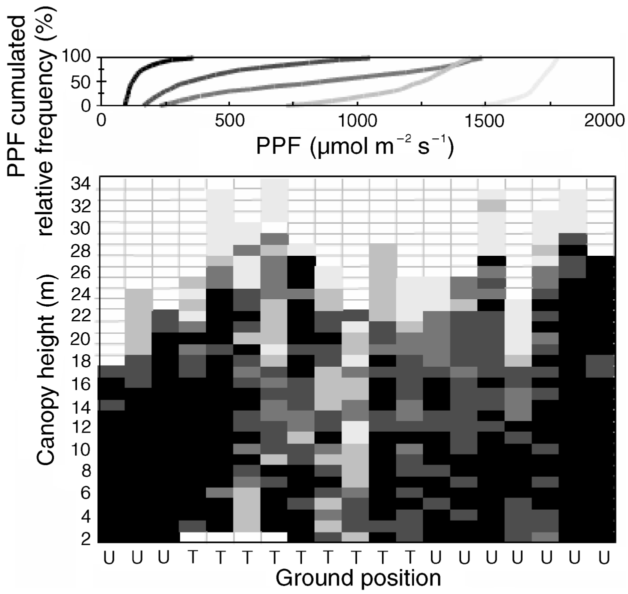

Figure 5. The K-means cluster analysis applied to the photosynthetic photon flux (PPF) dataset. (A) The five PPF cumulated relative frequency curves, each identified by a gray level, representing the five corresponding PPF clusters. Lighter gray indicates higher PPF. (B) Distribution of the five PPF clusters representing the PPF samples acquired in the undisturbed (U) and thinned (T) forest sections: each class is represented by a rectangle of a specific gray level according to the corresponding PPF cumulated relative frequency curve in (A).

m^2 s^{-1} was observed at 24.0 m height. A constant median of 100 µmol m^2 s^{-1} was computed in the bottom canopy until 3.0 m above the forest floor and a corresponding maximum 5–95th PPF percentile range of 500 µmol m^2 s^{-1} was assessed. In general, a positive skewness characterized the PPF distribution in the vertical transects through the undisturbed canopy.

In the thinned forest, the median PPF in the top fraction went from 1900 to 1400 µmol m^2 s^{-1} (computed at 28.0 m canopy height); the downward PPF medians decreased until 14.0 m canopy height varying from 1400 to 400 µmol m^2 s^{-1}, and in the bottom canopy the median PPF fluctuated between 400 and 200 µmol m^2 s^{-1}. Excluding the upper-canopy fraction, consistent 5–95th PPF percentile ranges were found in both the middle and bottom canopy fractions with a maximum of 1700 µmol m^2 s^{-1} (Figure 6B). A fluctuating negative/positive skewness was associated with the PPF distributions in the top canopy down to about 22.0 m height, whereas a consistent positive skewness in PPF distributions was observed at the lower-canopy levels.

Canopy directional leaf strata based on PPF inversion model

The relative frequency of *L* classes associated with the PPF vertical profiles shown in Figure 4 are plotted in Figure 7. Figure 7A shows *L* classes from 7.0 to 1.0, with the interval from 7.0 to 4.0 mostly represented. In contrast, Figures 7B–D show *L* classes fluctuated from 6.0 to 1.0, reflecting the corresponding heterogeneity in PPF.

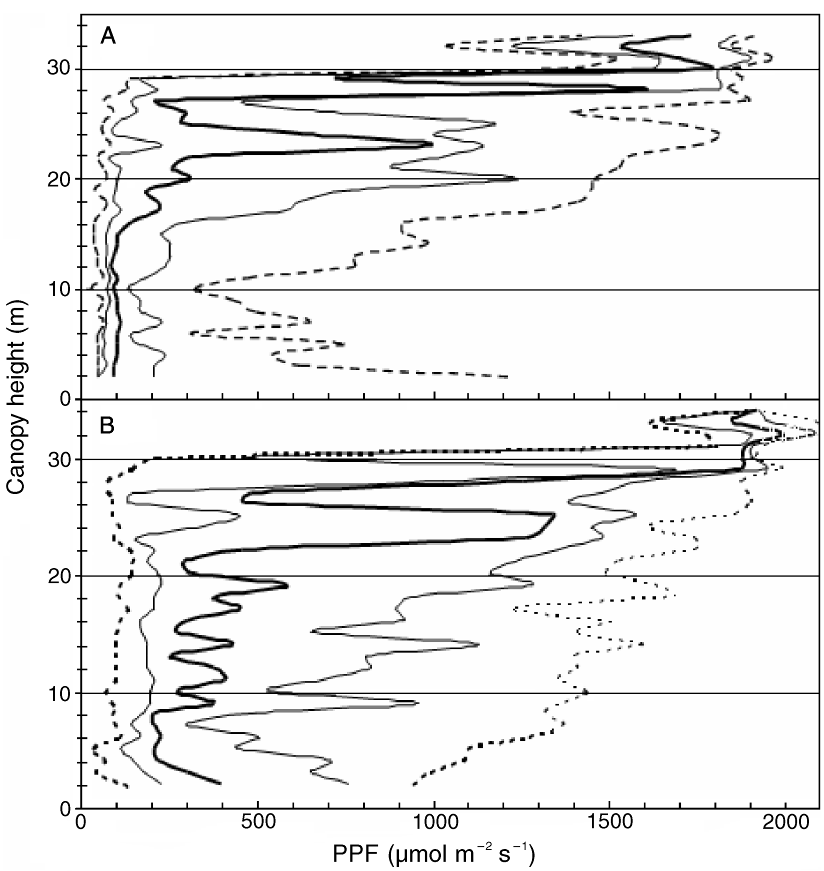

Figure 6. Effects of canopy height on the percentiles of photosynthetic photon flux (PPF) distribution in the (A) undisturbed and (B) thinned forest sections. The 5th (left dashed line), 25th (left continuous line), 50th (thick continuous line), 75th (right continuous line) and 95th (right dashed line) percentiles are graphed. Percentiles between canopy heights are interpolates.

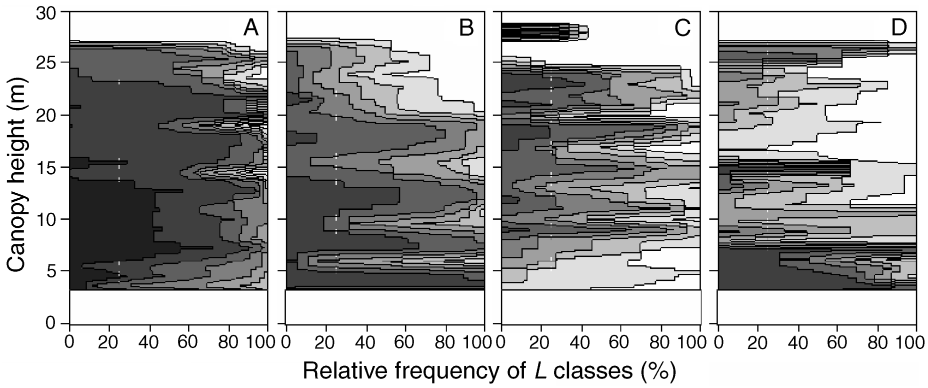

Figure 7. Contour plots showing the relative frequency of directional leaf strata (L) classes associated with the light values of the canopy vertical transects shown in Figure 4. The gray scale corresponds, from light gray to black, to seven increasing L classes with amplitude of 1.0 each. Background color (white) represents the relative frequency of sunlit positions (L = 0) above the vegetation, and within the canopy. Values between canopy height increments are interpolates.

The results of the K-means cluster analysis applied to the L dataset are shown in Figure 8. The undisturbed canopy had leaf strata classes ranging from 1.0 to 6.5, whereas the L classes in the bottom and middle layers of the thinned canopy mostly ranged from 1.0 to 4.5.

The 5, 25, 50, 75 and 95th percentiles representative of the L extracted at the different canopy heights are shown for both the undisturbed (Figure 9A) and thinned (Figure 9C) forest sections. A generally wide and consistent variability in L was found in the bottom, middle and almost all the top canopy layers in both forest sections.

In the undisturbed canopy, L medians of about 6.5 were computed from 3.0 m until about 15.0 m above the forest floor; decreasing medians from 6.0 to 1.5 were calculated between 15.0 and 24.0 m height. At higher elevations, the L medians increased up to 4.5 (at 24.0 m height) followed by a sharp decrease. In general, the L distribution of the undisturbed understory exhibited a slight negative skewness; whereas the L distribution of the top canopy had a variable positive/negative skewness (Figure 9A). In the undisturbed tree canopy, the contribution of the sunlit positions to the total number of PPF locations monitored was negligible in the bottom fraction, and it increased to 4.0% at 15.0 m, and to 24% at 24.0 m (Figure 9B).

The thinned canopy showed L medians fluctuating between 4.5 and 3.5 from 3.0 m to about 15.0 m above ground; the medians oscillated from 3.5 to 1.0 between 15.0 and 24.0 m height; and at higher elevations the L medians increased up to about 3.0 followed by a rapid decline. In general, no skewness characterized the leaf strata distribution in the thinned bottom- and middle-canopy layers, whereas a positive skewness in the L distribution was observed in the higher-canopy layers (Figure 9C). In the thinned forest section, the relative contribution of sunlit positions (L = 0) to the total number of PPF locations measured increased from the lower canopy to the canopy top: in particular, it was about 20% at 15.0 m and about 60% at 24.0 m (Figure 9D).

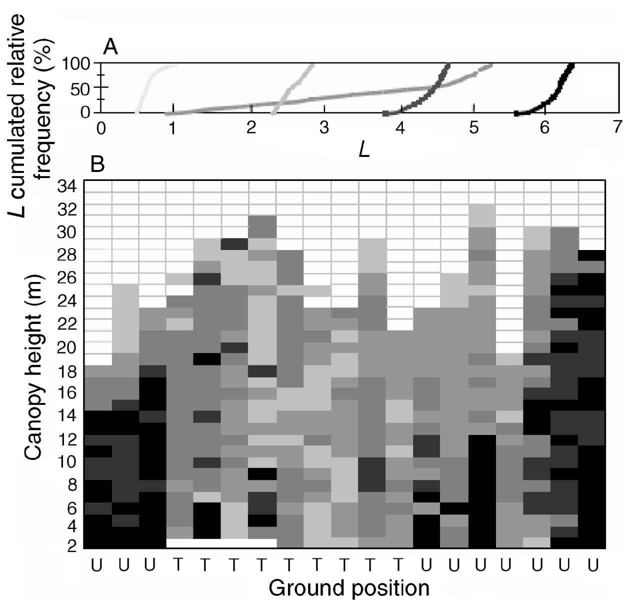

Figure 8. The K-means cluster analysis applied to the canopy directional leaf strata (L) dataset. (A) The five cumulated relative frequency distributions, each one identified by a gray level, representing the corresponding L classes. Lighter gray levels correspond to classes with higher photosynthetic photon flux. (B) Distribution of the five L clusters representing the L samples extracted in the undisturbed (U) and thinned (T) forest sections: each class is represented by a rectangle of a specific gray level according to the corresponding L cumulated relative frequency curve in (A).

Corroboration of extracted canopy directional leaf strata

Comparisons among the canopy leaf strata computed for each undisturbed and thinned forest section based on values obtained by the LAI2000, litter traps and the Monsi-Saeki model inversion of PPF point values collected at 3.0 m height are shown in Table 1. In each forest section, the mean L computed at 3.0 m from the ground for each explored profile was used for comparison with the LAI values quantified indirectly and directly. Mean L quantified in the undisturbed canopy section corresponded to the mean LAI measured by the LAI2000, whereas a slightly lower mean LAI value was computed from the litter trap data. The mean L of the thinned canopy section corresponded to the mean litter trap LAI, but it was lower than the indirect optical mean LAI. In general, wider variability was observed in the canopy L inferred by the Monsi-Saeki model than in the LAI computed by the LAI2000 or from litter collection data.

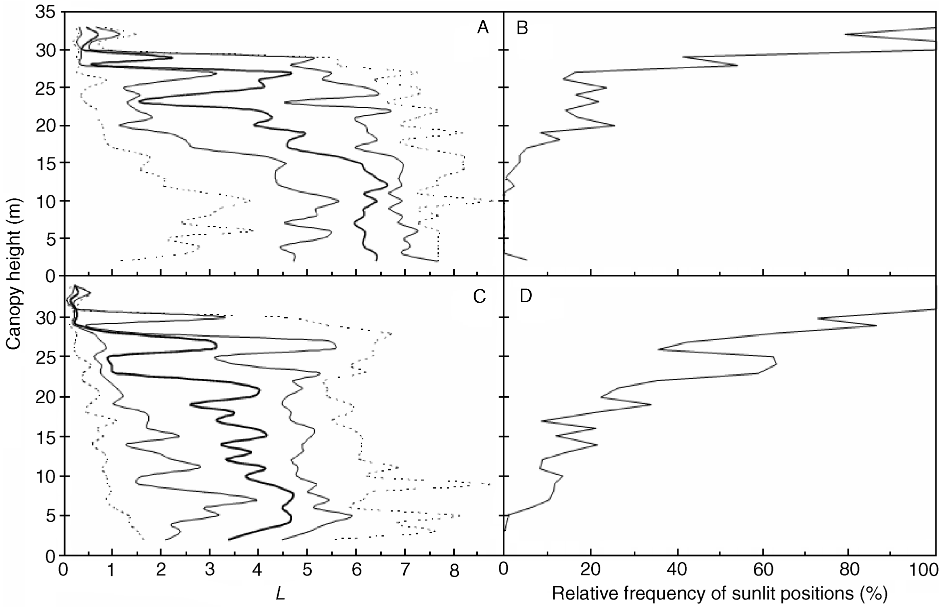

Figure 9. Percentiles representative of the leaf strata (L) distributions along a sunbeam direction at the different canopy heights in the (A) undisturbed and (C) thinned forest sections. The 5th (left dashed line), 25th (left continuous line), 50th (thick continuous line), 75th (right continuous line) and 95th (right dashed line) percentiles are shown. Relative frequency of sunlit positions (L = 0) at the different canopy heights in the (B) undisturbed and (D) thinned forest sections. Percentiles between canopy height increments are interpolates.

Discussion

Radiation measuring apparatus

Our data analysis indicates that the vertical PPF samplings in the thinned canopy and in the undisturbed top canopy did not adequately represent the shaded and penumbral values, corroborating the findings of Parker et al. (2002). We speculate that the within-foliage gaps explored in the bottom- and the middle-canopy fractions of the undisturbed forest were mostly shaded, whereas a significant presence of sunflecks was detected in the gaps explored in the thinned bottom- and mid-canopy layers. The direct beam and diffuse components of the within-canopy PPF have important effects on fundamental vegetation processes, so estimates of their contributions are needed for within-canopy functional modeling (Lexer and Hönninger 2001, Mariscal et al. 2004, Parker et al. 2005, Disney et al. 2006).

Table 1. Comparison between undisturbed and thinned canopies in mean (± standard error) leaf area index (LAI) estimated by direct (litter traps) and ground-based, optical remote sensing (LAI2000) techniques, and in leaf strata (L) along the sunbeam path (65 ± 7° elevation angle) estimated by inverting the PPF values (detected at 3.0 m height) using an adapted Monsi-Saeki model. The canopy structural parameters refer to forest sections. Abbreviation: n = number of observations used for comparison.

	Undisturbed canopy	*n*	Thinned canopy	*n*
LAI ± SE				
LAI2000	6.39 ± 0.56	10	5.58 ± 0.43	10
Litter traps	5.63 ± 0.43	10	4.20 ± 0.52	10
L ± SE				
Monsi-Saeki inversion	6.25 ± 0.80	10	4.13 ± 0.95	9

Our balloon apparatus could be modified for use in diverse forest canopy typologies and in various research contexts. For example, the helium-filled balloon could accommodate self-levelling sensor platforms (Mõttus et al. 2001), and various sensors could be substituted; e.g., sensors detecting a radiation waveband wider than that of photosynthetically active radiation, or sensors making it possible to compute the direct beam and diffuse fractions. By contrast, the use of a phytoactinometer (Mõttus et al. 2001) placed atop a balloon to sense direct radiation would be problematic. Although we measured within-canopy downwelling PPF only, the detection of upwelling reflected radiance (Zhao and Qualls 2005, 2006) could be also performed by an additional radiation sensor attached to a suitably shaped helium-filled chamber.

Within-canopy PPF attenuation

Along most parts of the explored vertical profiles, lower median PPF values and higher PPF variability were found in the thinned forest section than in the undisturbed forest section. In general, within-foliage radiation variability—which reflects the vegetation geometrical heterogeneity of the vegetation—is of great importance when mechanistically modeling canopy functions with radiation as the driving force (e.g., photosynthetic activity).

The frequency of intra-canopy sunlit positions retrieved at sun elevation angles between 58 and 72° was higher in the thinned forest than in the undisturbed forest. However, the magnitude of this difference may be overestimated given the possible absence of quantum flux measurements in dense vegetation zones in the thinned forest that prevented balloon access.

Radiation measurements over a longer time span than around noon would provide the data necessary to quantify the diurnal within-canopy light distribution. In addition, applying the proposed radiation sampling procedure under cloudy conditions would make it possible to characterize the within-canopy downward light penetration when the radiation is mostly diffuse. Under sunny conditions, within-canopy light distribution is more heterogeneous than under cloudy skies: deep in the canopy, some leaves that receive sunflecks are sunlit, whereas the others are shaded to different degrees.

Inference of canopy directional leaf strata from within-canopy PPF

All indirect methods of inferring canopy stratification have advantages and disadvantages, and simulated canopy structural data are not always directly comparable (Bréda 2003). In our study, only *L* (estimated at 3.0 m height) associated with sun elevation angles from 58 to 72°, and LAI computed in the same forest by ground-based optical remote sensing and by litter collection could be compared. There was general agreement between the Monsi-Saeki modeled *L* at 3.0 m height and the LAI estimates for both undisturbed and thinned oak–hickory forest sections. The wider variability shown by *L* at 3.0 m height compared with the indirectly and directly estimated LAI values indicates that the Monsi-Saeki model inversion may capture heterogeneity in canopy leaf strata more effectively than the other methods.

Under our experimental conditions, no underestimation of the Monsi-Saeki inverted canopy leaf strata—owing to the within-canopy diffuse PPF radiation collected by the quantum sensor—was observed. Generally, however, direct PPF measurements acquired through a forest stand are desired to infer *L*. By contrast, measuring global within-canopy PPF in orchard trees under a clear sky may be appropriate for *L* extraction, because broadleaf spatial distribution in canopies of only a few meters in height negates intra-foliage penumbral effects and within-canopy diffuse PPF (Giuliani et al. 2000).

The accuracy of the canopy directional leaf strata inferred by the Monsi-Saeki model inversion may be improved by using species-specific values of *K* computed for the upper-, middle- and lower-canopy layers (Thomas and Winner 2000), and accounting for diurnal and seasonal changes (Wang et al. 2007).

Our computed values of Ω were in agreement with published values for oak–hickory vegetation (Gower et al. 1999). However, Ω estimates should be performed for each forest species and for specific sites to increase the precision of LAI estimates (Weiss et al. 2004). In addition, diurnal and seasonal variations in Ω should be considered for dynamic canopy *L* inferences (Wang et al. 2004).

Limitations and applications of the within-canopy radiation sampling and data analysis procedure

Our semi-random sampling technique captured the within-canopy PPF heterogeneity in an oak–hickory forest. However, the effects of species assembly and age on the within-canopy PPF distribution were not considered, as was done by Parker et al. (2002). Under our experimental conditions, 9–10 vertical canopy profiles, generating a dataset of about 4000 PPF values, appeared sufficient to characterize the instantaneous downward PPF attenuation pattern in undisturbed and thinned forest sections. Only about 10 h was required to complete the radiation sampling.

Cluster analysis proved to be a convenient tool for describing within-canopy radiation and leaf strata distributions. Moreover, there is flexibility in the statistical procedure applied for data processing and analysis (e.g., spatial statistics could be involved), and the choice of the statistical technique is motivated by the aim of the investigation.

Progress in estimating plant productivity in vegetation typologies with a wide leaf spatial heterogeneity may be achieved by effective foliage stratification modeling (Ewert 2004). The use of LAI as a foliage structural parameter may be a poor choice for modeling canopy processes on a daily or shorter temporal scale because of its static nature in the short term (Oker Blom and Smolander 1988, Giuliani et al. 2000). Values of *L* at different sun elevations during the day would provide structural parameters useful for accurately estimating canopy intercepted quantum flux and CO_2 uptake (Brown and Parker 1994, Montgomery and Chazdon 2001). There is no mechanistic use of the inferred canopy directional *L* because it is impossible to identify intra-crown leaf area densities.

From a silvicultural perspective, the proposed PPF sampling–analyzing procedure may provide the experimental data needed to assess the relationship between canopy intercepted radiation and plant canopy growth. In addition, the effects of tree thinning on tree crown structure and on within-canopy light attenuation could be quantified, as shown in our study. An appropriate description of the spatial (both vertical and horizontal) and temporal distributions of radiation flux transmitted to the forest floor throughout the vegetation is required to study natural or managed plant regeneration (Messier et al. 1999, Brown et al. 2000, Prévost and Pothier 2003, Page and Cameron 2006), and to model forest succession (Pacala and Deutschman 1995, Lischke et al. 1998) processes.

In conclusion, the proposed semi-random procedure for sampling forest within-canopy global PPF along vertical transects effectively captures instantaneous light fluctuations. Appropriate modifications in the sensor-equipped helium-filled balloon apparatus would make it possible to extend its use to various vegetation typologies. The main contribution to the within-canopy light sampling procedure is the proposed statistical control to drive data acquisition. Multiple data processing solutions were employed to provide the statistical parameters describing the radiation fluctuations at contrasting vegetation levels. The acquired PPF data were inverted by a Monsi-Saeki model to extract the canopy leaf strata attenuating direct radiation. The computed within-canopy PPF distribution parameters and the inferred canopy *L* may be useful for empirical canopy photosynthetic models and for validating mechanistic models of within-canopy radiative transfer and canopy photosynthesis. The proposed within-canopy radiation sampling procedure could be used to characterize canopy structure, to estimate canopy growth and to predict forest renovation and succession.

Acknowledgments

Funding for this research was provided by the United States Forest Service cooperative agreement with Unit RWU NE 4153, and the USFS Joint Fire Sciences Program. We are grateful to Anagram Intl. (Eden Prairie, MN) for providing plastic material to build the balloons, and to Dr. Geoffrey G. Parker (Smithsonian Environmental Center, Edgewater, MD) for assistance in developing balloon protocols. In addition, we thank Drs. Nathan G. Phillips (Boston University) and Barbara J. Bond (Oregon State University) for assistance with the light sensor amplifier systems, Eugenio Magnanini (University of Bologna, Italy) for the scheme of the custom built height indicator and Mark Thornton (Ohio University) for building it, and Fabrizio Nerozzi (ARPA, Bologna, Italy) and Enrico Muzzi (University of Bologna) for assistance with statistical data analysis. Dr. Matti Mõttus (Tartu Observatory Tõravere, Tartumaa, Estonia) is acknowledged for reviewing the first draft of the manuscript.

References

Anderson, M.C. 1966. Stand structure and light penetration. II. A theoretical analysis. J. Appl. Ecol. 3:41–54.

Baldocchi, D. and S. Collineau. 1994. The physical nature of solar radiation in heterogeneous canopies: spatial and temporal attributes. *In* Exploitation of Environmental Heterogeneity by Plants. Eds. M.M. Caldwell and R.W. Pearcy. Academic Press, San Diego, pp 21–71.

Baldocchi, D.D., B.A. Hutchison, D.R. Matt and R.T. McMillen. 1985. Canopy radiative transfer models for spherical and known leaf inclination angle distributions: a test in an oak hickory forest. J. Appl. Ecol. 22:539–556.

Bréda, N.J.J. 2003. Ground based measurements of leaf area index: a review of methods, instruments and current controversies. J. Exp. Bot. 54:2403–2417.

Brown, M.J. and G.G. Parker. 1994. Canopy light transmittance in a chronosequence of mixed species deciduous forests. Can. J. For. Res. 24:1694–1703.

Brown, N., S. Jennings, P. Wheeler and J. Nabe-Nielsen. 2000. An improved method for the rapid assessment of forest understorey light environments. J. Appl. Ecol. 37:1044–1053.

Chen, J.M. 1996. Optically-based methods for measuring seasonal variation of leaf area index in boreal conifer stands. Agric. For. Meteorol. 80:135–163.

Chen, J.M. and J. Cihlar. 1995. Plant canopy gap size analysis theory for improving optical measurements of leaf area index. Appl. Optics 34:6211–6222.

Chen, J.M., P.M. Rich, T.S. Gower, J.M. Norman and S. Plummer. 1997. Leaf area index of boreal forests: theory, techniques and measurements. J. Geophys. Res. 102(D24):29,429–29,444.

Chen, J.M., C.H. Menges and S.G. Leblanc. 2005. Global mapping of foliage clumping index using multi angular satellite data. Remote Sens. Environ. 97:447–457.

Couteron, P., R. Pelissier, E.A. Nicolini and D. Paget. 2005. Predicting tropical forest stand structure parameters from Fourier transform of very high resolution remotely sensed canopy images. J. Appl. Ecol. 42:1121–1128.

Dessard, H. and A. Bar Hen. 2005. Experimental design for spatial sampling applied to the study of tropical forest regeneration. Can. J. For. Res. 35:1149–1155.

Disney, M., P. Lewis and P. Saich. 2006. 3D modeling of forest canopy structure for remote sensing simulations in the optical and microwave domains. Remote Sens. Environ. 100:114–132.

Efron, B. and R.J. Tibshirani. 1993. An introduction to the bootstrap. Monographs on statistics and applied probability, No. 57. Chapman and Hall, London, 436 p.

Eriksson, H., L. Eklundh, K. Hall and A. Lindroth. 2005. Estimating LAI in deciduous forest stands. Agric. For. Meteorol. 129:27–37.

Ewert, F. 2004. Modeling plant responses to elevated CO_2: How important is leaf area index? Ann. Bot. 93:619–627.

Gastellu Etchegorry, J.P., V. Demarez, V. Pinel and F. Zagolski. 1996. Modeling radiative transfer in heterogeneous 3D vegetation canopies. Remote Sens. Environ. 58:131–156.

Ghosh, S. and J.L. Innes. 1996. Comparing sampling strategies in forest monitoring programs. For. Ecol. Manage. 82:231–238.

Giuliani, R., F. Nerozzi, E. Magnanini and C. Fragassa. 2000. Ground monitoring the light shadow windows of a tree canopy to yield canopy light interception and morphological traits. Plant Cell Environ. 14:783–796.

Gower, S.T., C.J. Kucharik and J.M. Norman. 1999. Direct and indirect estimation of leaf area index, fAPAR, and net primary production of terrestrial ecosystems. Remote Sens. Environ. 70:29–51.

Hanan, N.P., G. Burba, S.B. Verma, J.A. Berry, A. Suyker and E.A.Walter-Shea. 2002. Inversion of net ecosystem CO_2 flux measurements for estimation of canopy PAR absorption. Global Change Biol. 8:563–574.

Houldcroft, C.J., C.L. Campbell, I.J. Davenport, R.J. Gurney and N. Holden. 2005. Measurement of canopy geometry characteristics using LiDAR Laser Altimetry: a feasible study. IEEE Trans. Geosci. Remote Sens. 43:2270–2282.

Hughes, B.D. 1996. Random walks and random environments, Vol. 1: Random walks. Oxford University Press, New York, 526 p.

Iverson, L.R., M.E. Dale, C.T. Scott and A. Prasad. 1997. A GIS-derived integrated moisture index to predict forest composition and productivity of Ohio forests (USA). Landsc. Ecol. 12:331–348.

Jacquemoud, S. 2004. Leaf optical properties. *In* Reflection Properties of Vegetation and Soil, with a BRDF Database. Eds. M. von Schönermark, B. Geiger and H.P. Röser. Wissenschaft and Technik Verlag, Berlin, 352 p.

Jonckheere, I., S. Fleck, K. Nackaerts, B. Muys, P. Coppin, M. Weiss and F. Baret. 2004. Review of methods for in situ leaf area index determination. Part I. Theories, sensors and hemispherical photography. Agric. For. Meteorol. 121:19–35.

Jones, H.G. 1992. Plants and microclimate: a quantitative approach to environmental plant physiology. 2nd Edn. Cambridge University press, Cambridge, 428 p.

Jurik, T.W. and H. Kliebenstein. 2000. Canopy architecture, light extinction and self-shading of a prairie grass, *Andropogon gerardii*. Am. Midl. Nat. 144:51–65.

Kaufman, L. and P.J. Rousseeuw. 1990. Finding groups in data. An introduction to cluster analysis. John Wiley and Sons, New York, 342 p.

Kitajima, K., S.S. Mulkey and S.J. Wright. 2005. Variation in crown light utilization characteristics among tropical canopy trees. Ann. Bot. 95:535–547.

Kucharik, C.J., J.M. Norman and S.T. Gower. 1998. Measurements of branch area and adjusting leaf area index indirect measurements Agric. For. Meteorol. 91:69–88.

Kucharik, C.J., J.M. Norman and S.T. Gower. 1999. Characterization of radiation regimes in nonrandom forest canopies: theory, measurements, and a simplified modeling approach. Tree Physiol. 19:695–706.

Law, B.E., A. Cescatti and D.D. Baldocchi. 2001. Leaf area distribution and radiative transfer in open canopy forests: implications for mass and energy exchange. Tree Physiol. 21:777–787.

Leblanc, S.G., R. Fernandes and J.M. Chen. 2002. Recent advancements in optical field leaf area index, foliage heterogeneity, and foliage angular distribution measurements. Proc. IGARSS 5: 2902–2904.

Leblanc, S.G., J.M. Chen, C. Fernandes, D.W. Deering and A. Conley. 2005. Methodology comparison for canopy structure parameters extraction from digital hemispherical photography in boreal forests. Agric. For. Meteorol. 129:187–207.

Lefsky, M.A., W.B. Cohen, G.G. Parker and D.J. Harding. 2002. Lidar remote sensing for ecosystem studies. BioScience 52:19–30.

Lexer, M.J. and K. Hönninger. 2001. A modified 3D patch model for spatially explicit simulation of vegetation composition in heterogeneous landscapes. For. Ecol. Manage. 144:43–65.

Lischke, H., T.J. Loeffler and A. Fischlin. 1998. Aggregation of individual trees and patches in forest succession models: capturing variability with height structured, random, spatial dispersions. Theor. Popul. Biol. 54:213–226.

Macfarlane, C., G. Andrew and C. Evangelista. 2007. Estimating forest leaf area using cover and fullframe fisheye photography: thinking inside the circle. Agric. For. Meteorol. 146:1–12.

Mariscal, M.J., S.N. Martens, S.L. Ustin, J. Chen, S.B. Weiss and D.A. Roberts. 2004. Light transmission profiles in an old growth canopy: simulations of photosynthetically active radiation using spatially explicit radiative transfer models. Ecosystems 5: 454–467.

Martens, S.N., S.L. Ustin and R.A. Rosseau. 1993. Estimating of tree canopy leaf area index by gap fraction analysis. For. Ecol. Manage. 61:91–108.

Messier, C., R. Doucet, J.C. Ruel, Y. Claveau, C. Kelly and M.J. Lechowicz. 1999. Functional ecology of advance regeneration in relation to light in boreal forests. Can. J. For. Res. 29: 812–823.

Miller, E.E. and J.M. Norman. 1971. A sunfleck theory for plant canopies. I. Lengths of sunlit segments along a transect. Agron. J. 63:735–738.

Monsi, M. and T. Saeki. 1953. Über den Lictfaktor in den Pflanzengesellschaften und sein Bedeutung für die Stoffproduktion. Jpn. J. Bot. 14:22–52.

Monteith, J.L. and M.H. Unsworth. 1990. Principles of environmental physics. Edward Arnold, London, 291 p.

Montgomery, R.A. and R.L. Chazdon. 2001. Forest structure, canopy architecture, and light transmittance in tropical wet forests. Ecology 82:2707–2718.

Mõttus, M. 2004. Measurements and modeling of the vertical distribution of sunflecks, penumbra and umbra in willow coppice. Agric. For. Meteorol. 121:79–91.

Mõttus, M., J. Ross and M. Sulev. 2001. Experimental study of ratio of PAR to direct integral solar radiation under cloudless conditions. Agric. For. Meteorol. 109:161–170.

Nobel, P.S. 1991. Physicochemical and environmental plant physiology. Academic Press, San Diego, 635 p.

Norman, J.M. and G.S. Campbell. 1989. Canopy structure. *In* Plant Physiological Ecology: Field Methods and Instrumentation. Eds. R.W. Pearcy, J. Ehleringer, H.A. Mooney and P.W. Rundel. Chapman and Hall, New York, pp 301–325.

Oker Blom, P. and H. Smolander. 1988. The ratio of shoot silhouette area to total needle area in Scots pine. For. Sci. 34:894–906.

Pacala, S.W. and D. Deutchman. 1995. Details that matter: the spatial distribution of individual trees maintains forest ecosystem function. Oikos 74:357–365.

Page, L.M. and A.D. Cameron. 2006. Regeneration dynamics of Sitka spruce in artificially created forest gaps. For. Ecol. Manage. 221: 260–266.

Parker, G.G. and M. Brown. 2000. Forest canopy stratification: is it useful? Am. Nat. 155:473–484.

Parker, G.G., P.J. Stone and D. Bowers. 1996. A balloon for microclimate observations within the forest canopy. J. Appl. Ecol. 33: 173–177.

Parker, G.G., M.M. Davis and S.M. Chapotin. 2002. Canopy light transmittance in Douglas fir/western hemlock stands. Tree Physiol. 22:147–157.

Parker, G.G., D.J. Harding and M.L. Berger. 2004*a*. A portable LIDAR system for rapid determination of forest canopy structure. J. Appl. Ecol. 41:755–767.

Parker, G.G., M.E. Harmon, M.A. Lefsky et al. 2004*b*. Three dimensional structure of an old growth *Pseudotsuga–Tsuga* canopy and its implications for radiation balance, microclimate and gas exchange. Ecosystems 7:440–453.

Parker, G.G., C. Tinoco Ojanguren, A. Martinez Yrízar and M. Maass. 2005. Seasonal balance and vertical pattern of photosynthetically active radiation with canopies of a tropical dry deciduous forest ecosystem in Mexico. J. Trop. Ecol. 21:283–295.

Phattaralerphong, J. and H. Sinoquet. 2005. A method for 3D reconstruction of tree crown volume from photographs: assessment from 3D digitized plants. Tree Physiol. 25:1229–1242.

Pierce, L.L. and S.W. Running. 1988. Rapid estimation of coniferous forest leaf area index using a portable integrating radiometer. Ecology 69:1762–1767.

Prévost, M. and P. Pothier. 2003. Partial cuts in a trembling aspen–conifer stand: effects on microenvironmental conditions and regeneration dynamics. Can. J. For. Res. 33:1–15.

Rich, P.M. 1990. Characterizing plant canopies with hemispherical photographs. Remote Sens. Rev. 5:13–29.

Roderick, M., G.D. Farquhar, S.L. Berry and I.R. Noble. 2001. On the direct effect of clouds and atmospheric particles on the productivity and structure of vegetation. Oecologia 129:21–30.

Ross, J. 1981. The radiation regime and the architecture of plant stands. Dr. W. Junk Publishers, The Hague, Netherlands, 391 p.

Sakai, T. and T. Akiyama. 2005. Quantifying the spatio temporal variability of net primary production of the understory species, *Sasa senanensis*, using multipoint measuring techniques. Agric. For. Meteorol. 134:60–69.

Shiver, B.D. and B.E. Borders. 1996. Sampling techniques for forest resource inventory. John Wiley and Sons, New York, 356 p.

Shlyakhter, I., M. Rozenoer, J. Dorsey and S.Teller. 2001. Reconstructing 3D tree model from instrumented photograph. IEEE Comput. Graph. Appl. 21:53–61.

Sinclair, T.R. 2006. A reminder of the limitations in using Beer's Law to estimate daily radiation interception by vegetation. Crop Sci. 46:2343–2347.

Smolander, S. and P. Stenberg. 2005. Simple parameterizations of the radiation budget of uniform broadleaved and coniferous canopies. Remote Sens. Environ. 94:355–363.

Spitters, C.J.T., H.A.J.M. Toussaint and J. Goudriaan. 1986. Separating the diffuse and direct component of global radiation and its implications for modeling canopy photosynthesis: I. Components of incoming radiation. Agric. For. Meteorol. 38:217–229.

Stoyan, D., W.S. Kendall and J. Mecke. 1995. Stochastic geometry and its applications. 2nd Edn. John Wiley and Sons, Chichester, 436 p.

Teske, M.E. and H.W. Thistle. 2004. A library of forest canopy structure for use in interception modeling. For. Ecol. Manage. 198: 341–350.

Thomas, S.C. and W.E. Winner. 2000. Leaf area index of an old growth Douglas fir forest estimated from direct structural measurements in the canopy. Can. J. For. Res. 30:1922–1930.

Vézina, P.E. and G. Pech. 1964. Solar radiation beneath conifer canopies in relation to crown closure. For. Sci. 10:443–451.

Wang, Y.P. 2003. A comparison of three different canopy radiation models commonly used in plant modeling. Funct. Plant Biol. 30:143–152.

Wang, Q., J. Tenhunen, A. Granier, M. Reichstein, O. Bouriaud, D. Nguyen and N. Bréda. 2004. Long term variations in leaf area index and light extinction in a *Fagus sylvatica* stand as estimated from global radiation profiles. Theor. Appl. Clim. 79:225–238.

Wang, W.-M., Z.-L. Li and H.-B. Su. 2007. Comparison of leaf angle distribution functions: effects on extinction coefficient and fraction of sunlit foliage. Agric. For. Meteorol. 143:106–122.

Weiss, M., F. Baret, G.J. Smith, I. Jonckheere and P. Coppin. 2004. Review of methods for in situ leaf area index (LAI) determination. Part II. Estimation of LAI, errors and sampling. Agric. For. Meteorol. 121:37–53.

Whitehead, D., J.C. Grace and M.J.S. Godfrey. 1990. Architectural distribution of foliage in individual *Pinus radiata* D. Don crowns and the effects of clumping on radiation interception. Tree Physiol. 7:135–155.

Wu, J., Y. Liu and D.E. Jelinski. 2000. Effects of leaf area profiles and canopy stratification on simulated energy fluxes: the problem of vertical spatial scale. Ecol. Model. 134:283–297.

Wulder, M.A. and S.E. Franklin. 2003. Remote sensing of forest environments. Concepts and case studies. Kluwer Academic Publishers, Boston, 519 p.

Zar, J.H. 1984. Biostatistical analysis. 2nd Edn. Prentice Hall, New Jersey, 718 p.

Zhao, W. and R.J. Qualls. 2005. A multiple layer canopy scattering model to simulate shortwave radiation distribution within a homogeneous plant canopy. Water Resour. Res. 41, W08409, doi: 10.1029/2005WR004016.

Zhao, W. and R.J. Qualls. 2006. Modeling of long wave and net radiation energy distribution within a homogeneous plant canopy via multiple scattering processes. Water Resour. Res. 42, W08436, doi:10.1029/2005WR004581.